THE EFFECTS OF SALT SPRAY ON COASTAL VEGETATION AT WILSON'S PROMONTORY, VICTORIA, AUSTRALIA

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Abstract

The vegetation of a coastal area exposed to strong winds carrying salt spray was investigated. Severe leaf-tip necrosis and the death of seaward shoots were found to be of widespread occurrence. Detailed studies of the succulence, salt content and internal morphology of leaves both from areas exposed to salt spray and from sheltered areas were made. These suggest that chloride toxicity caused by salt spray is a major factor determining the occurrence and growth of plants in exposed coastal areas.

Introduction

Salt spray as an ecological factor has received scant attention in Australia. Wood (1937) notes the occurrence of the halophytes *Disphyma australe* and *Suaeda maritima* on cliffs exposed to salt spray in South Australia, and similarly Willis (1962) in Victoria notes *D. australe* and *Salicornia australis* 'on littoral platforms and spray drenched ledges of rock'. The prevalence of succulent plants on exposed coastlines in general is well known (Smith 1957, Gillham 1960), and Smith (1957) notes that *Senecio lautus* becomes more succulent the nearer it grows to the sea. However, no reasons are suggested for this phenomenon.

Various adverse effects on the growth of shrubs on exposed coastlines have been observed. For example in Australia Pidgeon (1937) has noticed stunting of coastal shrubs, and attributed this to exposure to wind, without considering the precise mechanisms involved. Smith (1957) noticed stunting, and also the inhibition of seaward growth on coastal shrubs, and Osborn (1922) noted dead areas on the seaward sides of coastal shrubs; these phenomena were ascribed to 'wind pruning' or 'wind shearing' which presumably implies mechanical breakage of stems and leaves by wind.

Elsewhere the effect of salt spray on vegetation is well documented (Boyce 1954, Karschon 1958). It is the aim of this paper to describe the effect of salt spray on coastal vegetation near Tidal R., Wilson's Promontory.

The Study Area

Wilson's Promontory is the southernmost part of mainland Australia. The study area was located on its exposed W. coastline at Pillar Point, half a mile NE. of Tidal R. Pillar Point is a NE.-SW. trending granitic ridge, its NW. side (the study area) forming part of Leonard Bay, and its SE. side forming part of Norman Bay.

The field work was undertaken in September 1964 and June 1965 as part of the ecology practical work for Botany II, Botany IIA and Agricultural Botany II students of those years (University of Melbourne).

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The General Environment

The study area is adjacent to the area of vegetation mapped by Parsons (1966), and he has presented the relevant general climatic data. In brief the climate is maritime, with a mean annual rainfall of 43 in. The monthly prevailing wind direction is W. for all months except July (NW.), August (NW. and W.) and December (W. and NE.). Mean monthly wind speeds at 9 a.m. show no marked seasonal trends and vary from 13 to 18 miles per hour. Consequently the NW. side of Pillar Point is exposed to onshore winds, often of high speed, throughout the year, while its SE. side is much more sheltered.

Onshore winds were frequently observed to carry salt spray from the surface of the sea inland over the entire NW. side of Pillar Point.

The soils of the area are extremely variable. Parts of the lower slopes of the NW. side of Pillar Point have received an accession of wind-blown siliceous sand. Elsewhere the soils are derived from granite; they are often very shallow, and large outcrops of granite are common. Parsons (1966) has described the granitic soils of adjacent areas.

Vegetation

The vegetation of the NW. side of Pillar Point varies more or less continuously from the shoreline to the top of the ridge. However, at least four zones are readily discernible.

(1) Immediately behind the shoreline, pockets of shallow, poorly drained peaty soils occur on flat expanses of granite, around and between granite boulders, and near salt water rock-pools. The area regularly comes under the influence of wave splash, especially during conditions of high tides and strong onshore winds. The soil pockets carry a community of herbaceous perennials, many of which also occur in the salt marsh at the mouth of Tidal R. The principal species are *Cladium junceum, Samolus repens, Hydrocotyle muscosa, Disphyma australe, Leptocarpus brownii, Viola hederacea, Stipa teretifolia* and *Carex* sp. This community has not been investigated in detail here because it is almost certainly subject not only to a large amount of salt spray, but also to high levels of soluble soil salts due to a combination of wave splash and poor drainage.

(2) Leeward from zone (1), above the main wave-splash zone, on well-drained siliceous sands and shallow granitic soils, there is a narrow and rather discontinuous 'zone' in which the following plants are common: *Calocephalus brownii, Correa alba, Alyxia buxifolia, Helichyrysum gunnii, Persoonia juniperina, Grevillea lanigera, Banksia integrifolia, Tetragonia implexicoma, Helichrysum apiculatum, Scirpus nodosus, Leptospermum juniperinum, Pultenaea daphnoides, Senecio lautus,* and *S. elegans. Calocephalus brownii* forms a conspicuous fringe along the seaward edge of this zone, as it does elsewhere (Osborn 1922). Dense mats of prostrate *Goodenia ovata* occur in wet areas which appear to receive freshwater seepage from the higher parts of Pillar Point. These mats may also be subject to occasional wave splash.

(3) Further upslope, zone (2) is replaced by a heath (Wood & Williams 1960) dominated by *Leptospermum laevigatum. Leucopogon parviflorus* and *Casuarina stricta* are also common, and *Banksia integrifolia* and *Kunzea ambigua* occur occasionally. This zone occurs mainly on siliceous sands.

(4) On the upper half of the NW. side of Pillar Point the soils are mainly granitic, *Leucopogon parviflorus* disappears, and a number of species from *Casuarina pusilla-Leptospermum myrsinoides* heath (Parsons 1966) occur in the

L. laevigatum heath, including *Epacris impressa, Correa reflexa* and *Lepidosperma concavum.* At the NE. (landward) end of this highest zone, *Eucalyptus radiata* and *E. baxteri* occur as shrubs up to 10 ft high.

In zones (3) and (4), *Casuarina stricta* and *Kunzea ambigua* replace *L. laevigatum* heath on shallow soils around granite outcrops.

In contrast to these low-growing heath communities on the NW. side of Pillar Point, the SE. side carries a *L. laevigatum* thicket 15 ft high, as well as some other taller communities (Parsons 1966).

Growth Forms

Most of the shrubs growing along the seaward edge of zone (2) showed a strikingly asymmetric growth form. Branch development is much greater on the landward side of the shrubs than on the seaward side, and the canopy slopes up evenly from the seaward side, beginning at ground level and reaching heights of up to 6 ft on the landward side (Plate 1). Most of the shrubs are stunted compared to the size they attain in sheltered locations, and the main branches are usually curved in the shape of an arc pointing landward, and are more or less prostrate (Plate 1). Plan diagrams of shrubs growing in the most open parts of the community showed that these shrubs were markedly elliptical, the long axis of the ellipse running at right angles to the shoreline; in these cases growth is inhibited in all directions except directly landward.

This asymmetric growth form was observed in all the shrub and tree *species* on the exposed NW. side of Pillar Point. However, in more sheltered inland areas, plants of these species showed normal, symmetrical development. The same asymmetric growth forms occur in a wide range of exposed coastal areas (Boyce 1954). Several hypotheses have been advanced to explain the different rates of growth on the seaward and landward sides of plants and these have been reviewed to Boyce (1954). The most common hypotheses are:

(1) **Sandblasting.** Boyce (1954) observed some sandblasting damage to stems near ground level, but produced evidence that sand is not transported at sufficient height to cause asymmetric growth forms. At Pillar Point, the shoreline is granitic, and the areas of sand stabilized, so sandblasting is unlikely.

(2) **Desiccation** of seaward shoots and leaves by wind. At Pillar Point, no signs of wilting were observed. Although it appears that desiccation cannot cause asymmetric growth forms (Boyce 1954), exposure to wind may contribute to the general stunting of coastal plants by causing increased evapotranspiration or by causing stomatal closure and lowered photosynthesis.

(3) **Mechanical breakage by wind.** It was not possible to evaluate this hypothesis in the study area because of damage caused by tourists. However, other work indicates that in wind regimes like those of the study area, it is generally unimportant (Boyce 1954, Warren Wilson 1959), while in areas subject to hurricanes, mechanical breakage occurs but does not produce asymmetric growth forms (Boyce 1954).

(4) **Salt spray.** In the study area, the asymmetric growth forms were invariably accompanied by severe leaf-tip necrosis of seaward leaves; judging from the critical studies of Boyce (1954), it would appear that toxic amounts of chloride ions from salt spray were being deposited on the vegetation, inhibiting seaward growth and producing the asymmetric growth forms. This hypothesis was supported by observations of salt spray being carried by wind over the entire NW. side of Pillar Point, and by observations of numerous salt crystals on exposed leaves and stems in dry weather.

In addition to asymmetry and leaf-tip necrosis, large areas of dead shoots were present on the seaward sides of many shrubs. Also, many dead shoots protruded a few inches above the living canopy on the seaward side of these shrubs. The nearest leaves to these dead areas almost invariably showed leaf-tip necrosis, suggesting a common cause for the death of both shoots and leaf tips. Again, the work of Boyce (1954) has shown that such symptoms may be caused by chloride toxicity.

Leaf Morphology and Salt Content

As soluble salts in either soils or salt spray are known to enter plants and induce succulence (Boyce 1954), the morphology and salt content of a number of species were investigated in detail.

Methods

Leaf thickness was measured with a dial micrometer calibrated in divisions of 0·001 in.

Estimates of total soluble leaf salts were obtained from a conductance bridge (Jackson 1962). For this analysis 15 g. fresh weight of leaves were shaken in two changes of 100 ml. of distilled water for one min. each change on a 'Microid' flask shaker, to wash off salts present on the leaf surfaces. The final leaf washings did not contain detectable amounts of salts. The leaves were then ground up for two min. in 75 ml. of distilled water, using a 'Waring Blendor'. This suspension was filtered (Whatman No. 1 filter paper), the filtrate drawn up into a conductance cell, and its conductance measured on the conductance bridge.

Investigations

As a first step, the morphology and salt content of leaves of plants growing in the salt spray-exposed area were compared with those of leaves of plants of the same species from areas sheltered from salt spray, to see if any differences in succulence or salt content were present between them. Leaf succulence was measured as the thickness : area ratio, fresh weight : dry weight ratio and/or the fresh weight : area ratio.

Leaves were sampled from exposed shoots in comparable light regimes at the tops of the plants at both sites. Each population of leaves was then sorted into five

Table 1

Fresh weight : dry weight ratios, and conductance of leaf extracts of plants exposed to salt spray and of plants from areas sheltered from salt spray
All ratios are means of 50 leaves from 5 area classes

Species	Location			
	NW. side of Pillar Point (salt spray area)		Various locations sheltered from salt spray	
	Fresh weight : dry weight	Conductance (mhos x 10^6)	Fresh weight : dry weight	Conductance (mhos x 10^6)
Goodenia ovata	8·45	192	3·72	<9
Correa alba	4·47		2·99	
Myoporum insulare	11·72	833	5·94	500
Pultenaea daphnoides		169		<9
Eucalyptus radiata		147		109
Leptospermum laevigatum	2·39	250	2·54	143

area classes, each of ten leaves, and mean leaf thickness, fresh weight and dry weight obtained.

Leaf thickness and fresh weight measurements showed that the salt spray populations of *Goodenia ovata, Correa alba, Myoporum insulare* and *Pultenaea daphnoides* had thicker leaves in all area classes and higher fresh weights per unit

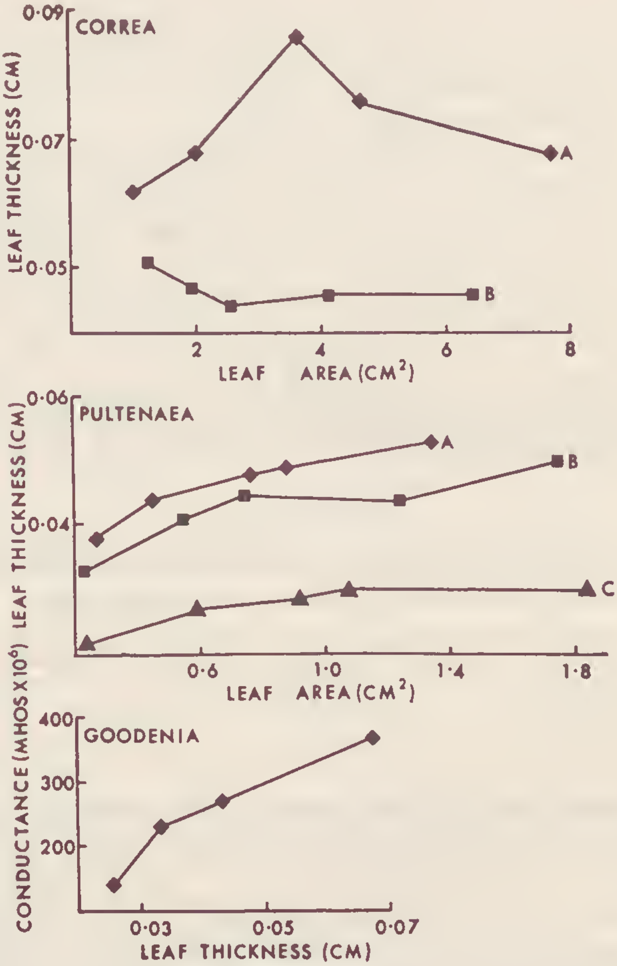

FIG. 1

Top: the relationship between leaf thickness and leaf area for leaves from the seaward side (graph A) and landward side (graph B) of a single shrub of *Correa alba* exposed to salt spray.

Middle: the relationship between leaf thickness and leaf area for three populations of *Pultenaea daphnoides.*

Graph A—Top of Pillar Point.
Graph B—Seaward edge of Pillar Point.
Graph C—Inland location sheltered from salt spray.

Bottom: the relationship between conductance of leaf extract and leaf thickness for leaves of *Goodenia ovata.*

area than the sheltered populations (Fig. 1). In addition, the salt spray populations of the three of these species tested had larger fresh weight : dry weight ratios (Table 1). The salt spray populations of all four species were more succulent than the sheltered populations in every comparison made with these three indices of succulence. Also, *Grevillea lanigera* and *Senecio lautus* were shown to have thicker leaves in all area classes in the salt spray area than in sheltered areas. By contrast, comparisons of populations of *Leptospermum laevigatum* using all three indices showed that this species does not become detectably more succulent in the salt spray area. However, the salt analyses showed that the leaves of the salt spray populations of every species examined contained higher concentrations of salts than those of the sheltered populations. (Table 1.)

These observations showed that the development of succulence was accompanied by high salt content. To try to relate succulence to salt content more closely, leaves of *Goodenia ovata* were divided into four thickness classes, and the salt content of each class was obtained. In this species, increasing thickness was accompanied by increasing salt concentration (Fig. 1), further indicating the causal relationship between salt content and succulence shown by Boyce (1954).

In an attempt to relate the observed succulence specifically to air-borne salts, leaves were collected from the seaward and landward sides of the outer canopy of an open grown shrub of *Correa alba*, and their weight, area, thickness and salt content determined as before. Leaf thickness, fresh weight and conductance were all consistently higher for the leaves from the seaward side of the shrub (Table 2;

TABLE 2

Fresh weight : dry weight ratios and conductance of leaf extracts of leaves from the seaward and leeward sides of a single plant of Correa alba *from the salt spray area*

All ratios are means of 50 leaves from 5 area classes

	Fresh weight: dry weight	Conductance (mhos x 10^6)
Seaward side of shrub	5·10	555
Leeward side of shrub	3·56	172

Fig. 1). This phenomenon is referred to as diamorphic succulence by Boyce (1954). The landward leaves were closely comparable in succulence with the leaves from the sheltered inland population analyzed earlier, showing that the succulence and high salt contents of leaves from the salt spray area are caused principally by air-borne salts, and that soil salts, which would produce equal succulence on seaward and landward leaves, were of less significance. Unpublished chloride analyses by Dr. D. H. Ashton and students have since shown for a number of the species investigated here, that leaves from salt spray populations contain higher chloride concentrations than leaves from sheltered populations, and also that seaward leaves of *Correa alba* contain higher chloride concentrations than leeward leaves from the same shrub.

Field observations had shown that asymmetric growth forms and leaf-tip necrosis of seaward leaves occurred over the entire NW. side of Pillar Point, suggesting that chloride toxicity from salt spray occurred over this entire area. This hypothesis was tested by sampling leaves of *Pultenaea daphnoides* simultaneously from the seaward edge of the shrub zone, from the top of Pillar Point, and from an inland location sheltered from salt spray. Succulence and salt content were closely comparable for the two Pillar Point populations, and much lower for the inland population, suggesting that salt spray is deposited over the entire NW. side of Pillar Point. In addition, leaves of *Eucalyptus radiata* from the landward edge of zone (4) showed typical chloride toxicity symptoms (Karschon 1958), and higher salt content than leaves from sheltered inland areas (Table 1).

The succulence of plants from the salt spray area was further investigated by microscopic inspection of transverse sections of leaves both from the salt spray area and from areas sheltered from salt spray. The species investigated were *Senecio lautus, Goodenia ovata, Correa alba* and *Grevillea lanigera*. Measurements of cell size with a micrometer eye-piece showed that in all these species, the increased succulence of the salt spray populations was caused by the hypertrophy of palisade and spongy mesophyll cells. In some cases, palisade cells were twice as long in leaves exposed to salt spray as in leaves sheltered from salt spray. Such hypertrophy is usually assumed to be a dilution phenomenon, i.e. an increased water uptake by the cell in response to a high concentration of salts derived from salt spray deposition (Boyce 1954). The thicker leaves of the salt spray populations of the species studied showed no evidence of any increase in the number of cell layers forming the lamina, in agreement with other work (Boyce 1954).

Discussion

The work described here and previous work (Boyce 1954, Karschon 1958) demonstrates that salt spray is a major factor determining the occurrence and growth of plants in exposed coastal areas. The most important effect of salt spray on vegetation is the deposition of large amounts of salt on aerial plant parts, frequently causing the death of shoots and leaves from chloride toxicity. The exposed coastal environment thus shows an important similarity to the salt marsh environment, where high concentrations of soil chloride are an important feature of the habitat. As a consequence, salt marsh plants like *Samolus repens* and *Disphyma australe*, which are adapted to high levels of soil chloride, occur also in badly drained parts of salt spray areas where they are subjected to high concentrations of chloride in both soil and air. However, large parts of salt spray areas differ from salt-marshes in having well-drained soils, so that they are not so closely related to them floristically. Nevertheless, at Pillar Point, two species from well-drained areas subjected to salt spray are also known from areas not subjected to salt spray but to high concentrations of soil chloride. These species are *Myoporum insulare*, which Parsons (1966) records from sheltered areas subjected to tidal inundation at Tidal R., and *Calocephalus brownii* which occurs 'in salt country inland' (Black 1957).

There appears to be a wide diversity of adaptations to air-borne salts in the salt spray community. *Calocephalus brownii* grows nearer to the sea than any of the other shrubs present in the area and very rarely shows any salt spray damage; it may therefore be the shrub most resistant to salt spray. The shoot system of this non-succulent species is densely branched, compact and hemispherical, and thus it is a typical cushion plant. Unlike the other shrubs in the area, it does not develop asymmetrically, except in the most severely exposed sites. The cushion habit of this plant presents a streamlined surface to wind and wind-borne salts. In addition, the shoots of *C. brownii* are completely covered by a fine white tomentum which may prevent salt spray from penetrating into leaves and stems. *Grevillea lanigera* is another species covered with fine hairs. Like *C. brownii*, it is practically confined to areas exposed to large amounts of salt spray. Another shrub, *Casuarina stricta*, has slender switch-like cladodes which readily align themselves parallel to the wind and in this way the area of shoot surface exposed to both wind and salt spray is greatly reduced.

The dominant shrub in most of the salt spray area is the sclerophyllous *Leptospermum laevigatum*. The present work has shown that this species does not develop detectable succulence in response to airborne salts. The work of Patton (1934) has shown that leaves of this species possess a very thick cuticle. This feature may lead to a reduced rate of entry of air-borne salts into leaves, and help to account for the presence of this species in salt spray areas, as suggested by Boyce (1954) for some non-succulent dune grasses of low salt content. The salt spray populations of the remainder of the species investigated were all more succulent than the populations from areas sheltered from salt spray. This difference in succulence was shown to be principally phenotypic in the case of *Correa alba*, in which marked diamorphic succulence was demonstrated. Such phenotypic variation caused directly by varying amounts of salt spray may also account for the observations by Smith (1957) and the present authors that *Senecio lautus* becomes more succulent the nearer it grows to the sea, and for similar differences in succulence for the other species investigated here. However the possibility of the development of 'salt spray ecotypes' within these species, like that found by Boyce (1954), cannot be discounted.

Eucalypts are absent from the salt spray area except at its most inland margin, where some scattered shrubs of *E. radiata* occur. These plants show an asymmetric growth form (Plate 1), a higher leaf salt content than sheltered inland plants (Table 1), and identical symptoms to those of other eucalypts of severe air-borne salt damage (Karschon 1958). It appears that the eucalypts occurring adjacent to the study area (Parsons 1966) are intolerant of salt spray, and that this factor excludes them from exposed coastal locations.

Previous Australian work attributing the asymmetric growth forms and smooth sloping crowns of exposed coastal shrubs to 'wind-pruning' and 'wind-shearing' (Osborn 1922, Smith 1957) now appears to be in error. In the present study, the close association of dead shoots with leaves showing chloride toxicity symptoms and having high salt content, strongly suggests that chloride toxicity is the cause of the characteristic growth forms of exposed coastal shrubs. This hypothesis is supported both by the previous work of Boyce (1954) on the role of air-borne salts in causing leaf and shoot death and subsequently asymmetric growth forms, and by the work cited in Boyce (1954) and Warren Wilson (1959) indicating that wind speeds in the study area would not be sufficient for any significant amount of mechanical breakage.

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Explanation of Plate

Plate 1

Top: Portion of the vegetation on the NW. side of Pillar Point. The coastline is approximately one chain directly to the right of the photograph. Two shrubs of *Leptospermum laevigatum* showing asymmetric growth forms are on the left; the one in the foreground also shows a large area of dead shoots on its seaward side. On the right are shrubs of *Calocephalus brownii* showing the cushion habit.

Middle: A small prostrate shrub of *Leptospermum laevigatum* on the NW. side of Pillar Point, showing a curved stem and dead seaward shoots. The ruler is one foot long.

Bottom: A shrub of *Eucalyptus radiata* on the top of Pillar Point showing dead seaward shoots and leaf tip necrosis of seaward leaves. *Kunzea ambigua* on the left of the photograph.